4-26-2019

Effects of deposited sediment and turbidity on survival and growth of Orbicella faveolata recruits

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NSUWorks Citation

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https://nsuworks.nova.edu/occ_stuetd/509.

Thesis of
Morgan Stephenson

Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science

M.S. Marine Biology

Nova Southeastern University
Halmos College of Natural Sciences and Oceanography

April 2019

Approved:
Thesis Committee

Major Professor: Joana Figueiredo, Ph.D.

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HALMOS COLLEGE OF NATURAL SCIENCES AND OCEANOGRAPHY

Effects of deposited sediment and turbidity on survival and growth of *Orbicella faveolata* recruits

By

Morgan Stephenson

Submitted to the Faculty of
Halmos College of Natural Sciences and Oceanography
in partial fulfillment of the requirements for
the degree of Master of Science with a specialty in:
Marine Biology

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Abstract

Corals are frequently exposed to elevated turbidity and deposited sediment caused from coastal construction, dredging, and/or beach renourishment. This study addresses the effects of turbidity and deposited sediment on the survival and growth of newly settled and 6-week-old *Orbicella faveolata* recruits and disentangles the effects of turbidity and deposited sediment. We conducted two experiments in which newly settled coral recruits were reared in one of ten different turbidity and deposited sediment treatments for five weeks (0 NTU/ 0 mg cm^{-2}, 3.4 NTU/ 0 mg cm^{-2}, 8.2 NTU/ 0 mg cm^{-2}, 16 NTU/ 0 mg cm^{-2}, 29.1 NTU/ 0 mg cm^{-2}, 0 NTU/ 0 mg cm^{-2}, 3.4 NTU/ 27.7 mg cm^{-2}, 8.2 NTU/ 50 mg cm^{-2}, 16 NTU/ 101 mg cm^{-2}, 29.1 NTU/ 220 mg cm^{-2}). The highest turbidity treatment in the absence of deposited sediment (29.1 NTU/ 0 mg cm^{-2}) had the best survival, suggesting that turbidity in the absence of sediment is beneficial to coral recruits, as it decreases harmful light levels. However, when recruits were exposed to both turbidity and deposited sediment, representative of normal coastal construction conditions, high turbidity when coupled with deposited sediment (16 NTU/ 101 mg cm^{-2} and 29.1 NTU/ 220 mg cm^{-2}) had negative effects on coral recruits. Based on the results from the first experiment, the experiment was repeated with six-week-old symbiotic recruits for two weeks to determine if the sensitivity to light and benefits of high turbidity were related to the presence of symbionts. Six-week-old recruits also had the highest survival in the highest turbidity treatment, suggesting that light sensitivity by coral recruits is not dependent on the presence of symbionts within the first six weeks post-settlement. While the low light associated with turbidity increases recruit survival, turbidity is a proxy for deposited sediment, which has negative effects on coral recruits. Based on the results from this study, regulations should prevent turbidity from exceeding 8.2 NTU to prevent excessive deposited sediment on coral reefs, and its deleterious effects on corals.

Keywords: turbidity, deposited sediment, dredging, coral, recruits

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Introduction

Coral reefs are economically and ecologically important, providing over 30 billion dollars to the global economy in goods and ecosystem services (Moberg and Folke 1999; Cesar et al. 2003). Coral reefs are home to a diverse range of species (Connell 1978). Although coral reefs only occupy 0.1% of all marine environments (Spalding and Grenfell 1997), they are home to 25% of all marine fish species (Spalding et al. 2001). The biodiversity on coral reefs supports fisheries and tourism worldwide, providing $5.7 billion and $9.6 billion, respectively, to the global economy (Cesar et al. 2003). More than 100 countries border coral reefs and the tens of millions of people that populate coasts rely on coral reef resources for their livelihood (Sadovy 2005). Also, along coastlines coral reefs serve as physical buffers and prevent wave action and coastal erosion (Kunkel et al. 2006). In addition, scientists have discovered promising biochemical compounds on coral reefs for treatment of common medical ailments, such as cancer, AIDS, and inflammation (Proksch et al. 2002).

Despite their importance, coral reefs are rapidly declining due to global and local stressors worldwide (Bellwood et al. 2004; Knowlton and Jackson 2008; Carilli et al. 2009). Rising greenhouse gas emissions have resulted in global ocean warming and acidification (Hughes et al. 2003). High sea temperatures cause corals to expel their symbiotic algae (coral bleaching), which decreases coral growth and reproduction, and often results in wide-spread coral death (Baird & Marshall, 2002; Hoegh-Guldberg et al. 2007; Hughes et al. 2018). Carbon dioxide in the atmosphere is absorbed by the ocean, reducing its overall pH and availability of carbonate ions, which decreases coral growth rates (Hoegh-Guldberg et al. 2007; Kroeker et al 2013). In addition to these global stressors, the input of excess nutrients into coastal water causes eutrophication and promotes macroalgal cover on coral reefs (Bell 1992; Fabricius 2005). Overfishing of herbivorous fishes removes grazers from the reef, which further facilitates macroalgal growth (Hughes et al. 2007). Regime shifts to algal-dominated reefs ultimately reduces coral recruitment and survival from competition and smothering (Ogden and Lobel 1978; Hughes et al. 2007). Coral reefs are also vulnerable to coastal construction, particularly dredging and beach renourishment projects. These activities increase water turbidity and deposited sediment, which have detrimental impacts on reefs (Erftemeijer et al. 2012). To maximize coral resilience to global climate change, it is imperative to control local stressors (Carilli et al. 2009; Fourney and Figueiredo 2017).

Turbidity is a measure of water ‘cloudiness’, or the intensity of light scattered by suspended particles in the water column, and is often measured in Nephelometric Turbidity Units (NTU). Coral reefs are exposed to natural variations in turbidity (Jouon et al. 2008). However, the sediment that occurs naturally on reefs is coarse and heavy, and thus, even during severe storms, turbidity levels do not remain high for a very long period of time, as the coarse sediment quickly settles out. Contrarily, the sediment generated during coastal construction is finer and remains in the water column for an extended period of time due to constant particle resuspension, which elevates turbidity (Erftemeijer et al. 2012). Turbidity in more pristine tropical reefs typically ranges from 0-3 NTU (Fichez et al. 2010; Fabricius et al. 2013). In South Florida, natural turbidity levels, range from 0-1 NTUs (Boyer & Briceno 2015), however, the Environmental Protection Agency (EPA) allows coastal construction projects to increase turbidity up to 29 NTU above background turbidity (U.S. EPA 1988), for the entire duration of the project.

Elevated turbidity from suspended particles has been shown to negatively impact adult corals by reducing their access to light (Fabricius 2005; Pollock et al. 2014; Miller et al 2016). Corals require light because they host algal dinoflagellates, *Symbiodiniaceae,* that provide corals with energy for survival. Reduced light diminishes the ability of the *Symbiodiniaceae* to photosynthesize. As a result, elevated turbidity has been shown to reduce adult coral growth and calcification rates, increase respiration rates, and decrease survival (Telesnicki and Goldberg 1995; Kleypas et al. 1999, Flores et al. 2012). The ability of corals to cope with turbid water is species-specific and varies across geographic locations (Anthony and Connolly 2004). Some species show deleterious effects of elevated turbidity within 24 h of exposure, while other species may not see impacts until a few days or weeks after (Kendall et al. 1983; Negri et al. 2009). Switching from autotrophy to heterotrophy when light transmittance is low (Anthony and Larcombe 2000) is a common resistance mechanism. Corals living in areas where turbidity naturally fluctuates due to storms or runoff can better withstand turbidity caused by anthropogenic actions (Nieuwaal 2001). However, the constant resuspension of particles into the water column can increase turbidity for an extended period of time, which can eventually threaten even tolerant species.

Coastal construction also increases the amount of sediment depositing onto the corals, blocking access to light, obstructing polyps from collecting food, and in high quantities, smothering them (Rogers 1990; Fabricius 2005; Erftemeijer et al. 2012). To slough off excess sediment from their polyps, corals can secrete mucous. However, chronic sedimentation and mucous production will exhaust corals and deplete their energy reserves, which may already be depleted by low light conditions (Riegl and Branch 1995; Fabricius and Wolanski 2000; Crabbe and Smith 2005; Sheridan et al. 2014). Impaired heterotrophic feeding further depletes the corals' energy reserves, significantly reducing coral growth and survival (Riegl and Branch 1995; Crabbe and Smith 2005; Fabricius 2005; Erftemeijer et al. 2012; Sheridan et al. 2014). When the deposited sediment has a high proportion of fine particles, particularly silt, and is nutrient rich, it promotes bacterial growth and creates an anoxic environment around the corals in which shortly leads to tissue necrosis and coral death (Weber et al. 2006).

The detrimental effects of sediment and turbidity are even more severely felt in coral recruits. High sediment exposure has been shown to have negative impacts on the early life history stages of corals, decreasing fertilization success, larval development, and settlement (Jones et al. 2015). After settlement, the small size of recruits (<1 mm diameter) makes them more vulnerable to elevated sedimentation (Fabricius et al. 2003; Jones et al. 2015; Moeller et al. 2017). Even low amounts of deposited sediment will be sufficient to block the coral polyps and thus prevent them from feeding. As recruits have very little energy reserves, they cannot withstand long period of starvation. Equally, their small size makes them more vulnerable to smothering from high deposited sediment. Natural survival rates of coral recruits are already very low (Smith 1992; Penin et al. 2010), thus any increase in mortality due to increased turbidity and sedimentation can be completely jeopardize the persistence of the population.

While much of the damage caused by turbidity (via reduced light) and sedimentation (via blocked polyps) is determined by the *Symbiodinacea* within coral tissues, the establishment of this relationship is variable among coral recruits, which may lead to variability in relative susceptibility to these stressors for different individuals and species. For broadcast spawning species, recruits often acquire their algal symbionts from the water column or nearby sediment (i.e. horizontal transmission) within the first few weeks of settling (Adams et al. 2009). In the time before the acquisition of symbionts, it is possible that turbidity might be beneficial for recruits, as it can reduce the risk of tissue damage from dangerously high light levels (Robbins 2018). Symbionts contain mycrosporine-like amino acids (MAAs), which can protect corals from high light (Yuyama and Hidaka 2004). Since newly settled aposymbiotic recruits do not yet possess these MAAs, they are extremely vulnerable to light, thus the light low light associated with turbidity might be beneficial to these recruits. However, turbidity on reefs is always accompanied by an increase in deposited sediment (Pavanelli and Bigi 2005), which might hinder the heterotrophic abilities of pre-symbiotic recruits. Without the *Symbioniacea* to compensate for this loss of food energy, the additive effects of turbidity and deposited sediment will likely negatively impact pre-symbiotic recruits over all. Alternatively, in coral recruits that have established symbionts, the opposite might be true: high turbidity might impair the photosynthetic efficiency of these MAA containing symbionts, causing their residency within the coral tissues to become parasitic to the host and ultimately impair their survival or growth, while also potentially aiding in energy production (though diminished) at times of sedimentation and a cessation of heterotrophic feeding. Previous studies have demonstrated that newly settled coral recruits are more sensitive to both high deposited sediment and high light than adults (Fabricius 2005; Abrego et al. 2012). However, it is unknown how the effects of high turbidity and/or deposited sediment might differ between recruits because of the presence/absence of *Symbiodiniaceae*.

This study investigates the singular effects of turbidity and the combined effects of turbidity and deposited sediment on newly settled *Orbicella faveolata* recruits. This assessment is important to determine the threshold tolerance of coral recruits to elevated turbidity and the associated deposited sediment levels during coastal construction activities. Additionally, the experiments were performed on both newly settled (pre-symbiotic) and six-week-old (symbiotic) coral recruits to determine if the presence of *Symbiodiniacea* influenced the response to these stressors. The outcomes of this study will assist local managers to regulate allowable turbidity and associated deposited levels during coastal construction activities, such as dredging of ports or beach renourishment. For coral populations to persist in the future, it is important that regulations of maximum allowable turbidity levels are suitable for the survival and growth of both adult and coral recruits.

Methods

Study Species

Orbicella faveolata (previously named *Montastraea faveolata*; Fig 1 and 2), are boulder corals common along the Florida reef tract and throughout the Caribbean (Chiappone and Sullivan 1996). This species has severely declined within the past 20 years and is listed as endangered by the International Union for Conservation of Nature (Aronson et al. 2008) and threatened by the Endangered Species Act. Colonies can grow up to 10 m in diameter and occupy shallow habitats, 1-10 m depth (Szmant et al. 1997). It is a hermaphroditic broadcast spawner and typically spawns 2.5 hours after sunset 6-7 days after the full moon in August and/or September (Sánchez et al. 1999).

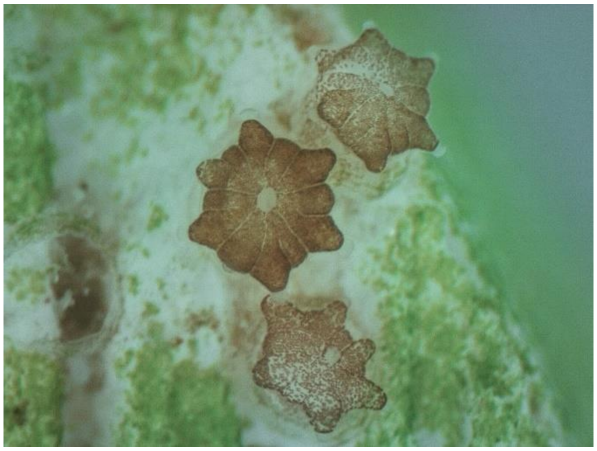


Figure 1. Six-week-old *Orbicella faveolata* recruits

Figure 2. Adult *Orbicella faveolata* colony

Spawning and Larval Settlement

Orbicella faveolata gametes were collected in the field on August 2, 2018 in Key Largo, Florida. Gamete bundles were collected by temporarily placing a mesh tent with a collection container attached to the top over the adult coral colonies when setting was observed. Once the corals released gamete bundles, which are positively buoyant, they floated to the surface and into the collection container. The eggs and sperm from different colonies were combined and after approximately 120 minutes a series of dilutions using a gravy separator were performed in order to prevent polyspermy. The embryos were reared to the larval stage under ambient conditions (29°C) in polystyrene containers at a density of <1 embryo/mL with 1μm filtered, sterilized seawater. Water changes were performed daily.

Once the larvae became competent (i.e. ready to settle and metamorphose, about 2 days after fertilization), settlement tiles were added to the polystyrene containers and sprinkled with crustose coralline algae, a known settlement cue for coral larvae. Approximately 1000 larvae were poured into each container, which were then placed in water baths with a heater set at ambient temperature (29°C) and two submersible pumps to homogenize the temperature (Fig 3). After 48 h, the tiles were checked for settlement and metamorphosis. Each tile was photographed under an Olympus stereoscope with a LC-20 Olympus camera, and the program cellSens was used to measure the coral surface area. The tiles were then randomly assigned to an experimental treatment.

Figure 3. Polystyrene containers containing settlement tiles and coral larvae in a water bath.

Sediment Collection and turbidity measurements

The sediment was collected in the Guy Harvey Oceanographic Center’s boat basin from the top 10-20 cm of the sediment layer via SCUBA and was placed in a drying oven at 70°C for a minimum of 72 h to remove moisture and kill any microscopic organisms. The sediment was then passed through a series of sieves and classified based on grain size composition according to the Udden-Wentworth Sediment Classification Scale (Wentworth 1922) and then all grain sizes were combined again to mimic the natural sediment composition of the boat basin. This assured that the sediment grain size composition was constant throughout each treatment (0.23% >2000 μm, 3.84% 500-2000 μm, 50.81% 180-500 μm, 37.01% 63-180 μm, 8.19% <63 μm).

A preliminary study was performed to determine how much sediment should be added to each tank in order to reach the desired turbidity level and to determine the respective deposited sediment. A known amount of sediment was added to a tank with two submersible pumps and the turbidity levels were measured hourly with a LaMotte 2020we turbidimeter in Nephelometric Turbidity Units for one week before and after 100% and 50% water changes due to resuspension of sediment. The relationship between sediment added and associated turbidity was calculated using a linear regression, which was used to determine the amount of sediment necessary to reach the desired turbidities (3.75, 7.5, 15, and 30 NTU). Once the sediment necessary for the desired turbidity levels was calculated, the sediment was added to a tank where turbidity was measured before and after water changes for 96 hours. The values obtained following the 50% water change at 48 hours were replicated again at 96 hours and 120 hours in order to observe how the turbidity changed over of the course of a week within each treatment (Fig 4a). Boxplots were created and the interquartile range (middle 50% of the observations) was calculated to determine the range of turbidity the recruits were exposed to for 50% of the week (Fig 4b). The low turbidity treatment had a median of 3.4 NTU, with an interquartile range of 2.16-4.7 NTU, intermediate turbidity had a median of 8.2 NTU, with an interquartile range of 5.55-10.67, the high turbidity treatment had a median turbidity of 16 NTU with an interquartile range of 12.11-19.91, and the allowable turbidity had a median of 29.1 NTU with an interquartile range of 24.34-33.85. To measure deposited sediment associated with each desired turbidity, sediment traps (i.e. petri dish) were placed into the tanks before sediment was added. Sediment was then added to the tanks and after 24 h, the petri dishes were removed and the sediment within each dish was dried and weighed to determine the amount of sediment deposited per cm^2 in 24 hours. The average deposited sediment associated with the turbidity values were 27.7, 50, 101, 220 mg cm^{-2} for 3.4, 8.2, 16, and 29.1 NTU, respectively.

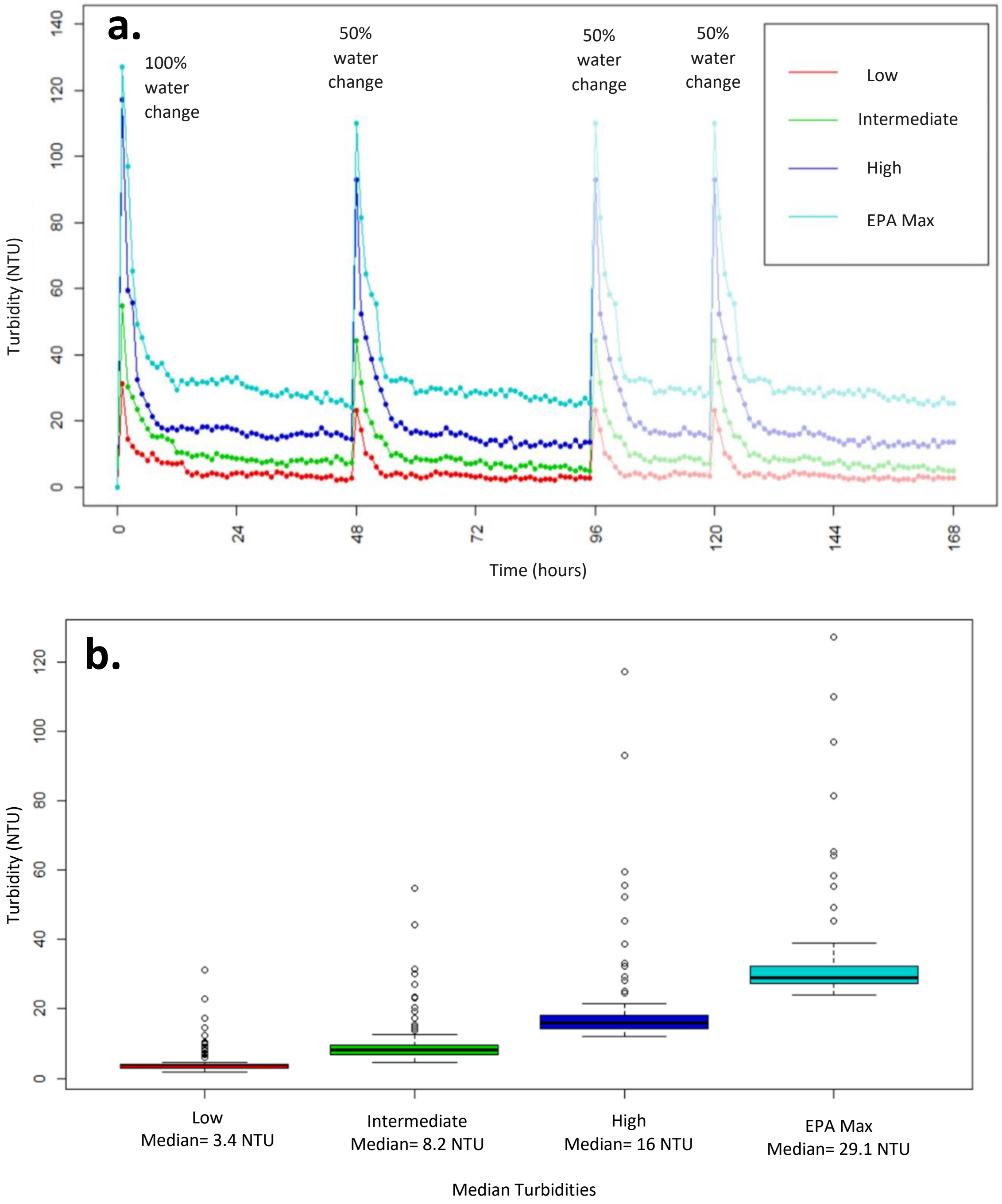


Figure 4. Turbidity variation in all experimental treatments (a) turbidity measured in each treatment over one week with one 100% water change and three 50% water changes. b) Boxplots of the four different turbidity treatments with the interquartile range representing the turbidity corals were exposed to 50% of the time.

Experimental Design

To assess the effect of turbidity and deposited sediment concentration on newly settled coral recruits, newly settled corals were reared under 10 different sedimentation/turbidity levels: 0 NTU/ 0 mg cm^{-2}, 0 NTU/ 0 mg cm^{-2}, 3.4 NTU/ 0 mg cm^{-2}, 3.4 NTU/ 27.7 mg cm^{-2}, 8.2 NTU/ 0 mg cm^{-2}, 8.2 NTU/ 50 mg cm^{-2}, 16 NTU/ 0 mg cm^{-2}, 16 NTU/ 101 mg cm^{-2}, 29.1 NTU/ 0 mg cm^{-2}, 29.1 NTU/ 220 mg cm^{-2}. Each treatment was replicated in two tanks, with 30 coral recruits per tank (N = 60/treatment) (Fig 5). These turbidity levels and their associated deposited sediment values were chosen because undisturbed reefs exposed to natural sediment have a turbidity of 0-1 NTU and the EPA currently allows an increase up to 29 NTU above background turbidity during dredging, making the total allowable turbidity ~30 NTU (U.S. EPA 1988; Boyer & Briceno 2015).

Within each tank, 30 recruits on tiles were suspended upside-down (i.e. exposed to turbidity only, free of deposited sediment) and 30 recruits on tiles were placed on the tank bottom (exposed to turbidity and deposited sediment) (Fig 6). The tiles suspended upside down were attached to plastic egg crates with Velcro and wires attached to the tank kept the crates stable. This allowed for the tiles to be suspended upside down in the water while still capable of removal for weekly measurements. Aqua Illumination Sol LED lights were set so that all corals regardless of their orientation and in the absence of sediment, were exposed to measure 20 µm photons.$cm^{-2}s^{-1}$, typical of crevices were larvae typically settle (Frade et al. 2008); this was possible because the tank used is white and the suspended egg crate tray with upside down corals slightly shaded the corals facing upwards. Each tank contained a heater which was set to ambient temperature and two SunSun JP-032 submersible pumps to mimic natural water movement and homogenize temperature in the tank. In addition, an adult coral fragment was placed in each tank in order to introduce *Symbiodiniacea* to the newly settled aposymbiotic recruits. Fifty percent water changes were implemented 3 times a week and a 100% water change was performed once a week. Temperature and salinity were measured daily and reverse osmosis water was added as needed to maintain salinity at 35 ppt. Recruits were fed rotifers *ad libitum* weekly.

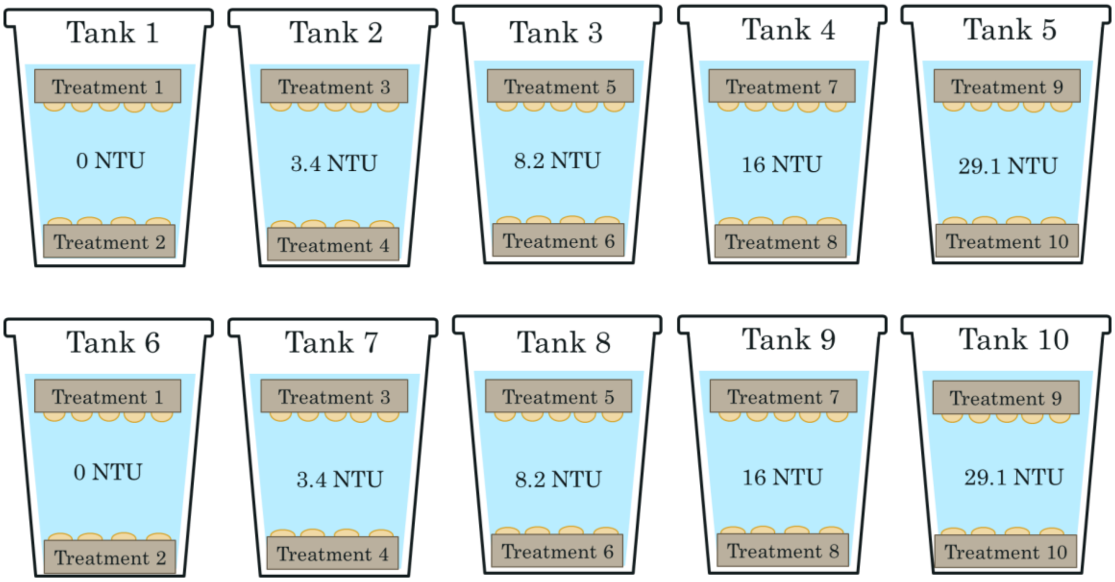


Figure 5. Experimental set up. Tiles with recruits on the tank bottom were exposed to sedimentation and turbidity, while tiles with recruits suspended upside down were exposed to only turbidity.

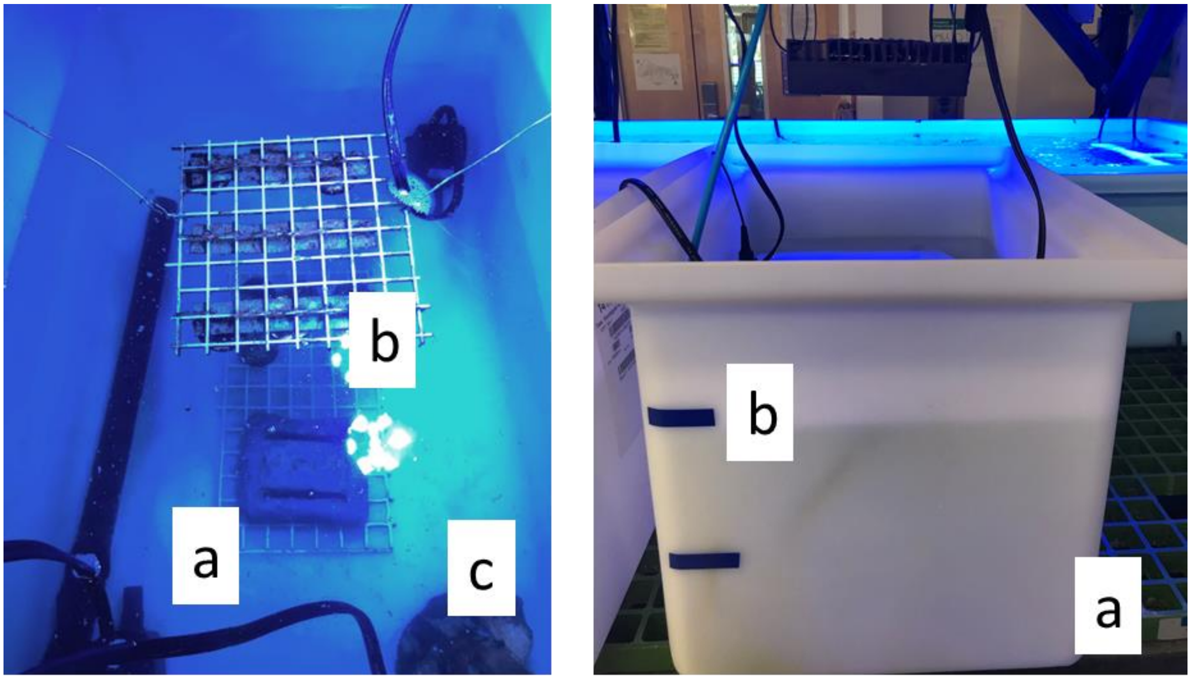


Figure 6. Tank set up where *a* is the tank bottom where recruits were exposed to both turbidity and deposited sediment, *b* is the egg crate containing tiles suspended upside down, where recruits are exposed to turbidity and no deposited sediment, *c* is an adult coral that is expected to act as a source of *Symbiodiniaceae.*

The survival and growth of the newly-settled recruits were measured weekly for 5 weeks. Growth was measured under an Olympus microscope using LC-20 camera and cellSens imaging software. When observing the recruits under the microscope, any macroalgae present was scrapped away as best as possible to prevent overgrowth.

To determine if coral recruits with established symbionts showed a different response to turbidity, this experiment was repeated with six-week-old recruits which contained *Symbiodiniacea* (visible through their coloration) exposed to turbidity only, free of deposited sediment. These recruits come from the same batch of larvae as the ones used in the first experiment and after settlement, were reared in a 453 L recirculating raceway containing a UV sterilizer, protein skimmer, bioballs, calcium reactor, and phosphate reactor. These corals recruits were exposed to light levels of 10 µm photons.cm^{-2}s^{-1} and the raceway was maintained at ambient temperature. After six weeks, the recruits were randomly placed in the experimental tanks. The tanks were setup as mentioned previously, and survival measurements were recorded weekly for two weeks.

Data Analysis

For both newly settled and six-week-old recruits, the effect of turbidity and deposited sediment concentration on recruit survival was determined using Mantel-Haenszel log rank tests (event of interest: mortality). If the factor was determined to be significant, a post-hoc multiple comparisons test was performed. To determine if there was a tank effect on recruit survival, a two-way repeated measures ANOVA was conducted. The test the effect of deposited sediment and turbidity on recruit growth rates, we first determined the model that best fit the growth curve (exponential model). Then to test the effect of deposited sediment and turbidity on growth we compared a model which parameters were independent of treatment with a model with parameters fit to each treatment, using a log-likelihood ratio test. All data analyses were conducted using the statistical software R (R Core Team 2016).

Results

Turbidity alone without deposited sediment significantly increased survival of newly settled recruits ($p < 2x10^{-16}$) (Fig 7). Recruits in the highest turbidity (29.1 NTU) treatment had the best survival, with 70.5% survival after 5 weeks. There was 100% mortality by week 3 in the 0 NTU treatment, by week 4 in the 16 NTU treatment, and by week 5 in the 3.4 NTU treatment. The 8.2 NTU treatment had 98% mortality by week 5, with one recruit alive by the end of the experiment. Survival was not dependent on tank effects ($p>0.05$).

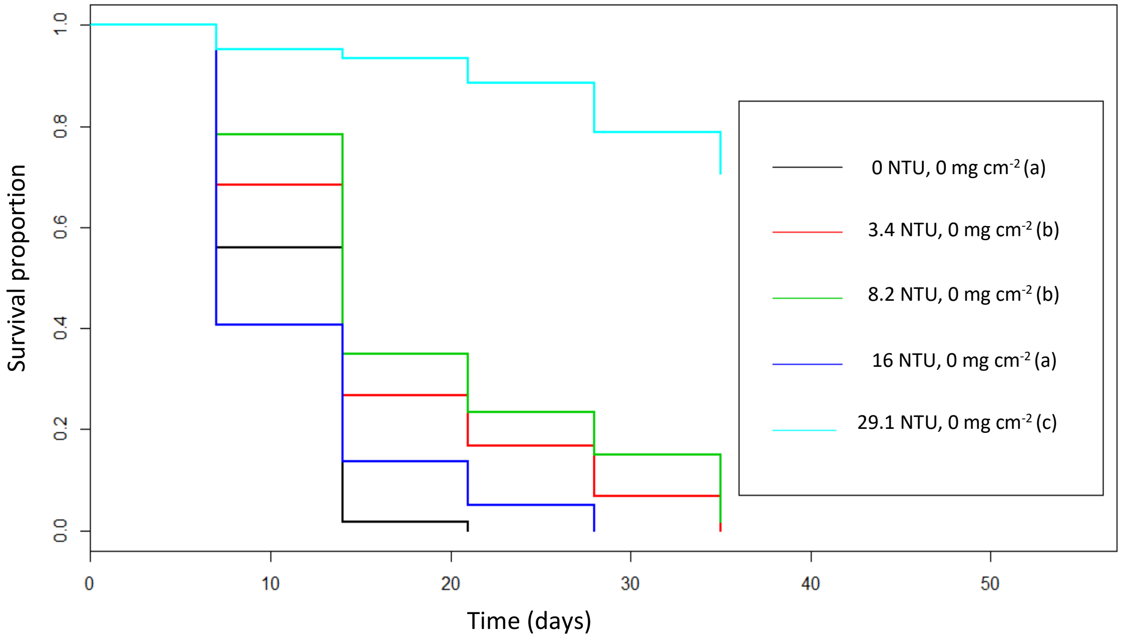


Figure 7. Survival curves for the newly settled *O faveolata* recruits at different turbidities (in the absence on deposited sediment). The different colors represent the five median turbidity treatments, and the different letters represent significantly different treatments.

Turbidity together with deposited sediment significantly affected the survival of newly settled recruits ($p < 2x10^{-16}$) (Fig. 8). Survival was the lowest in the absence of turbidity and deposited sediment (0 NTU/0 mg cm^{-2}), with 100% mortality by week 2. Among the treatments with deposited sediment, the 3.4 NTU/27.7 mg cm^{-2} and the 8.2 NTU/50 mg cm $^{-2}$ had the best survival at the end of the five weeks, with 33% and 32% survival, respectively; higher turbidity and deposited sediment led to lower survival rates (7.93% and 9.67% survival for 16 NTU/101 mg cm^{-2} and 29.1 NTU/220 mg cm^{-2}, respectively).

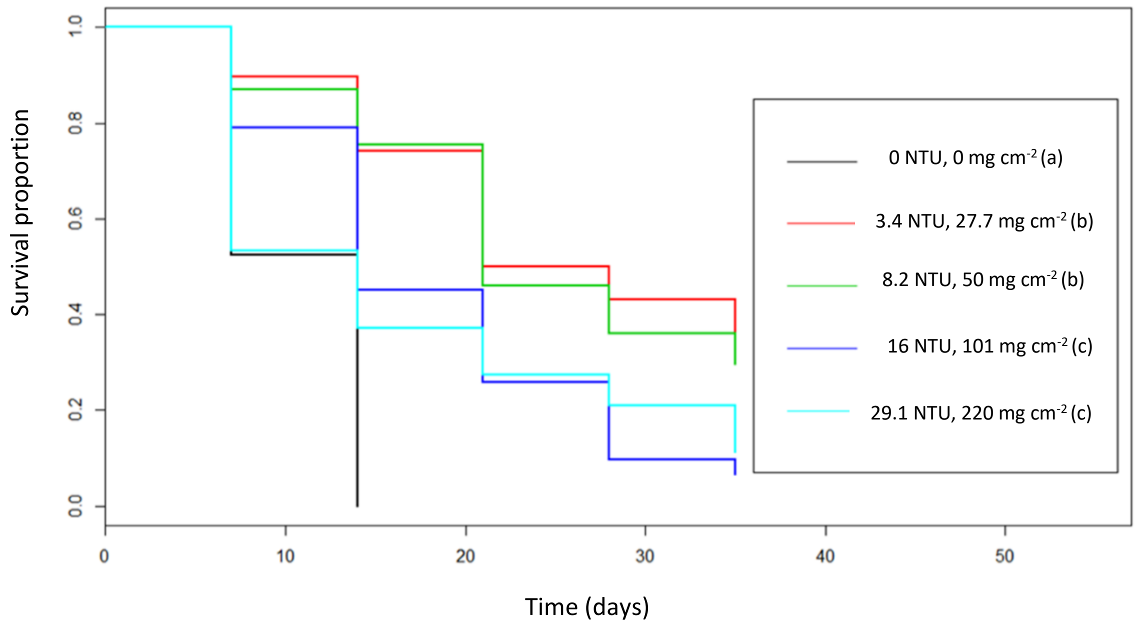
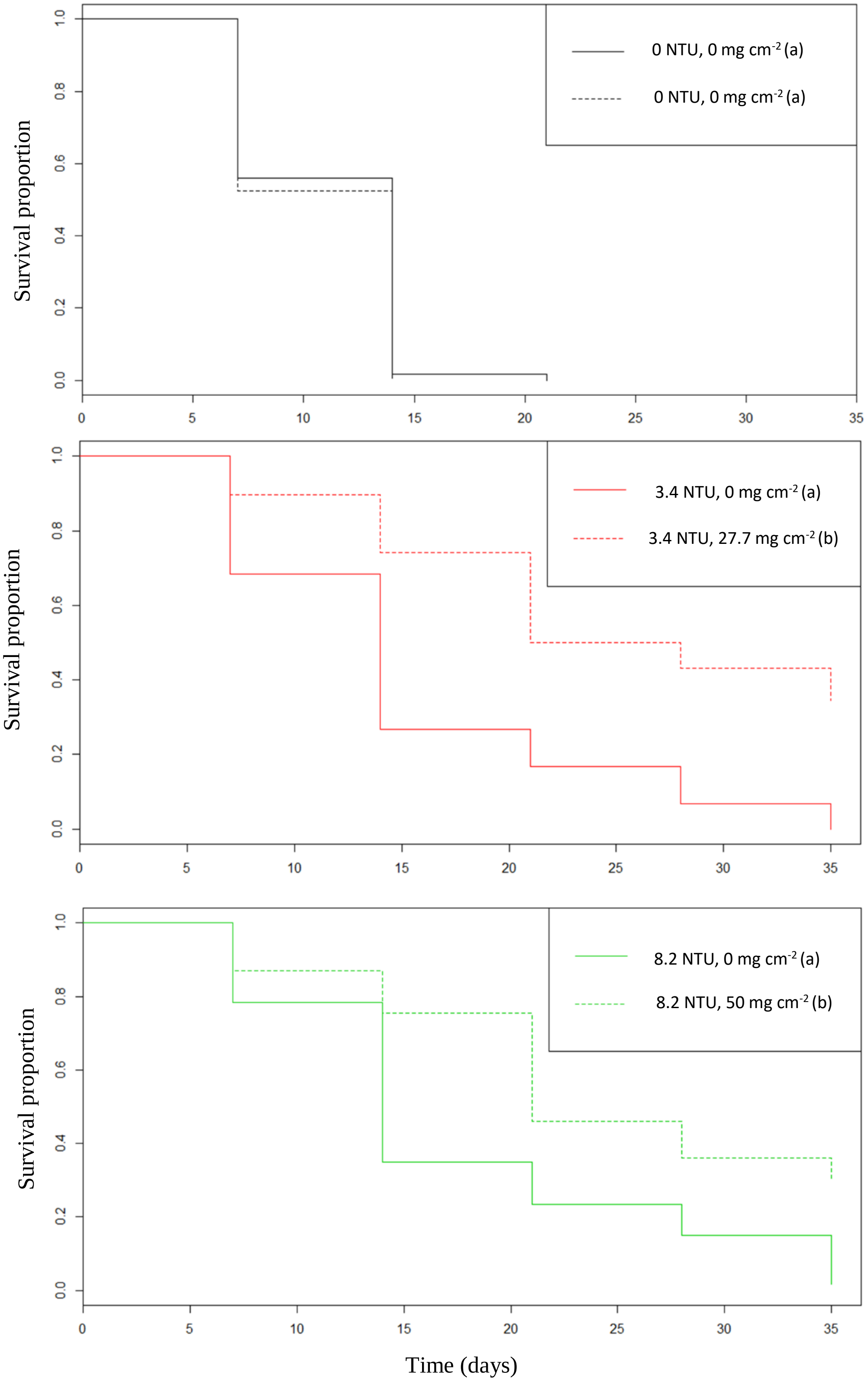


Figure 8. Survival curves for the newly settled recruits exposed to both turbidity and sedimentation. The different colors represent the five different median treatments, and the different letters represent significantly different treatments.

In the treatments with the highest turbidity, survival was significantly higher when no sediment was deposited on top of the corals (29.1 NTU/ 0 mg cm^{-2}) than when a large amount of sediment was deposited on top of the coral recruit (29.1 NTU/ 220 mg cm^{-2}) (p=2x10^{-14}). At lower levels of turbidity (3.4-16 NTU), survival was significantly higher in the treatments with deposited sediment (3.4 NTU/27.7 mg cm^{-2}, 8.2 NTU/50 mg cm^{-2}, and 16 NTU/ 101 mg cm^{-2}) than in treatments without deposited sediment (3.4 NTU/0 mg cm^{-2}, 8.2 NTU/0 mg cm^{-2}, and 16 NTU/0 mg cm^{-2}) (p=3x10^{-9}, 1x10^{-5}, 2x10^{-6}, respectively; Fig. 9).



Survival proportion
1.0
0.8
0.6
0.4
0.2
0.0
0 NTU, 0 mg cm-2 (a)
0 NTU, 0 mg cm-2 (a)
0
5
10
15
20
25
30
35
Survival proportion
1.0
0.8
0.6
0.4
0.2
0.0
3.4 NTU, 0 mg cm-2 (a)
3.4 NTU, 27.7 mg cm-2 (b)
0
5
10
15
20
25
30
35
Survival proportion
1.0
0.8
0.6
0.4
0.2
0.0
8.2 NTU, 0 mg cm-2 (a)
8.2 NTU, 50 mg cm-2 (b)
0
5
10
15
20
25
30
35
Time (days)

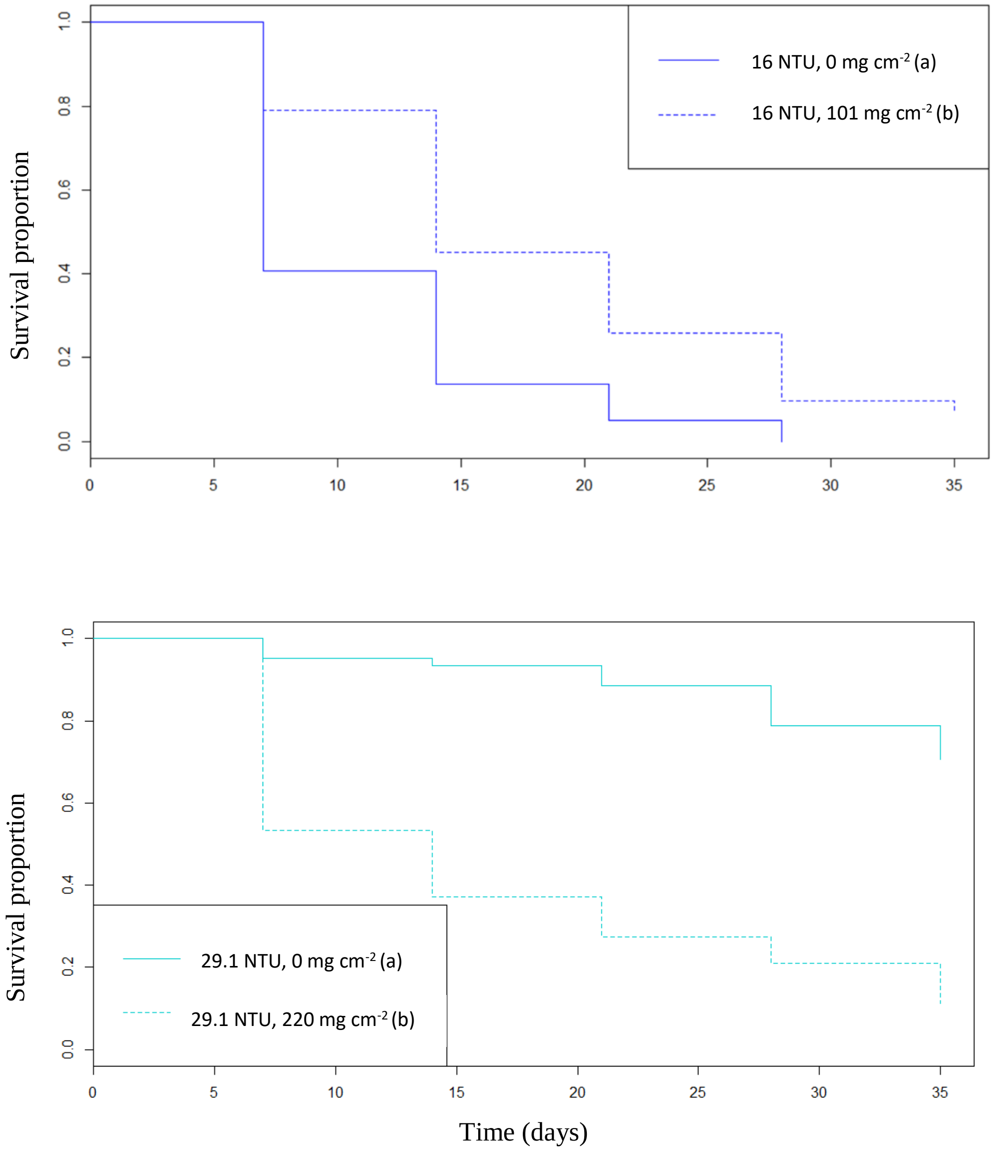


Figure 9. Recruit survival proportion in turbidity and the associated deposited treatments compared to recruit survival in turbidity in the absence of deposited sediment treatments. Different letters represent significantly different treatments.

Both turbidity in the absence of deposited sediment and turbidity coupled with deposited sediment did not significantly affect newly settled recruit growth rates ($p>0.05$, Fig. 10). Growth rates were more variable in the early weeks of the experiment with little variance in growth rates by the last week.

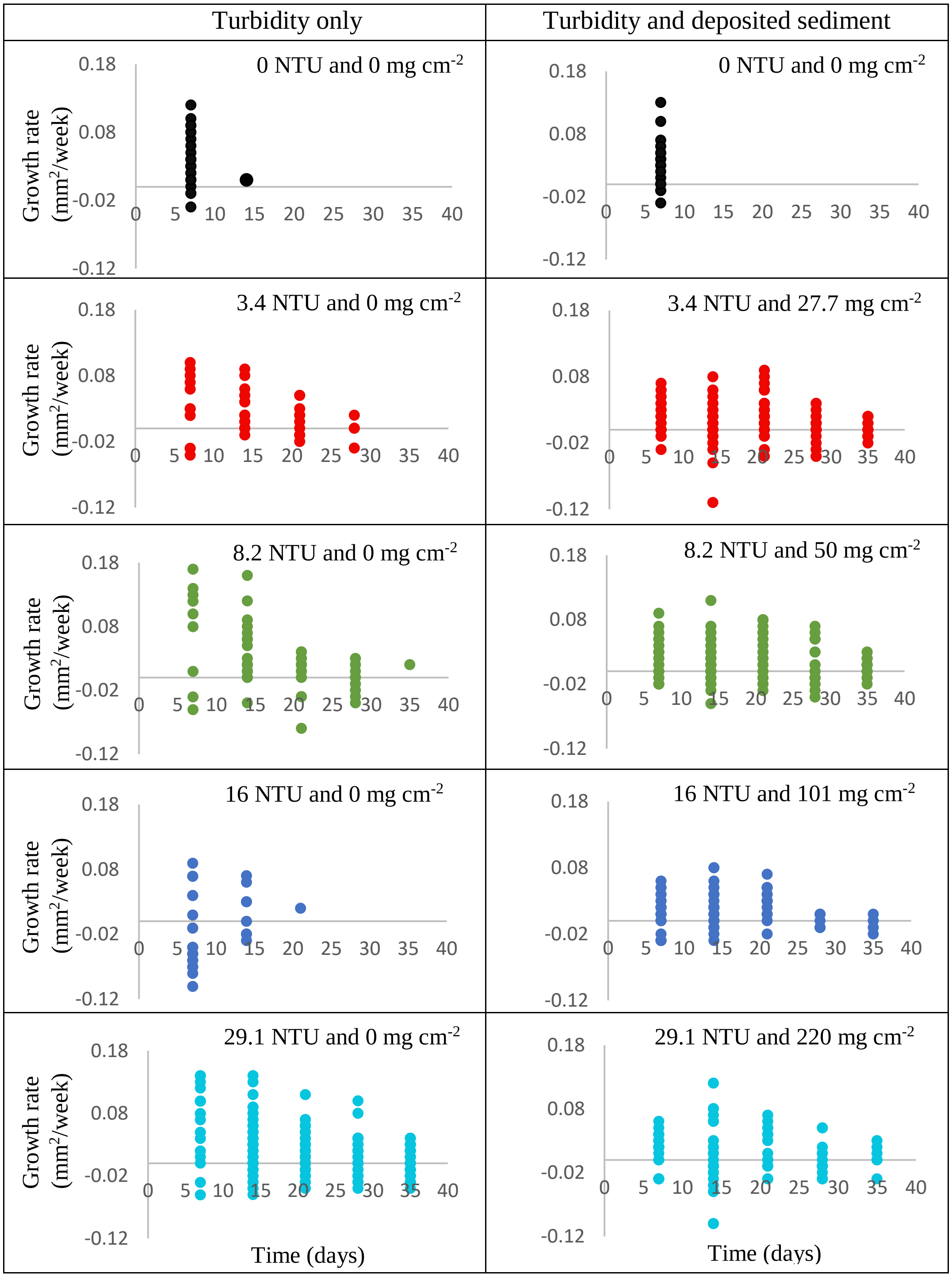


Figure 10. Weekly growth rates (calculated as the different from one week to the previous) of surface area of newly settled recruits in each treatment (each row represents one turbidity, left: treatments without sediment; right: treatments with deposited sediment).

For six-week-old recruits with *Symbiodiniaceae*, turbidity alone (without deposited sediment) significantly increased survival ($p=1x10^{-6}$) (Fig. 11). The 0 NTU and 3.4 NTU treatments had the highest mortality, with 63% and 60% mortality by the end of the second week, respectively. Similar to the newly settled recruits, the 29.1 NTU treatment had the highest survival, with only 6.7% mortality after two weeks.

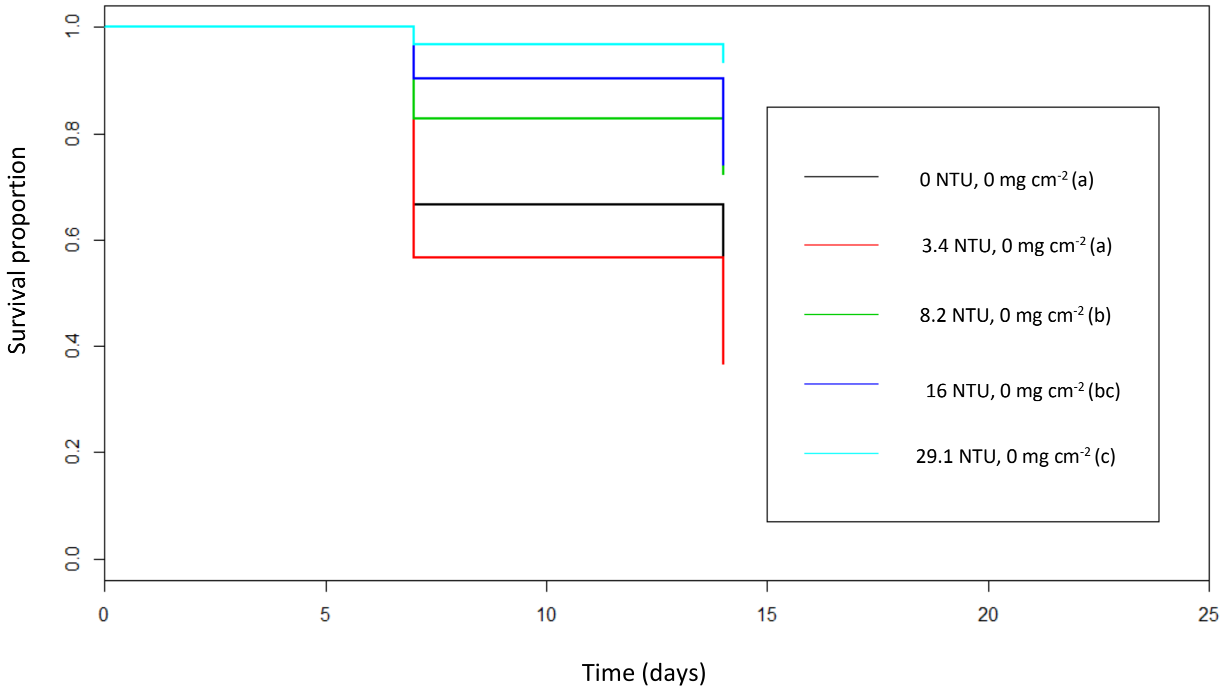


Figure 11. Survival curves for the six-week-old coral recruits with *Symbiodiniaceae* exposed to different levels of turbidity (without deposited sediment) for two weeks. The different colors represent the five different turbidity treatments, and the different letters represent significantly different treatments.

Discussion

Higher turbidity alone had a positive effect on the survival of newly settled and six-week-old *Orbicella faveolata* recruits, but when coupled with deposited sediment, as it had the opposite effect. Increased mortality at low turbidity levels suggests that both aposymbiotic and symbiotic recruits are sensitive to light levels. While the low light associated with turbidity was advantageous, turbidity coupled higher quantities of sediment deposited on top of the coral recruits were detrimental. However, the complete absence of deposited sediments also resulted in high recruit mortality; survival was optimal at low levels of deposited sediment, suggesting the presence of some sediment may somehow be beneficial potentially by preventing the growth of macroalgae that outcompete the coral recruits. Within the short time frame of this study (6 weeks), growth rates were minimal and thus were not significantly affected by turbidity nor deposited sediment.

In the absence of deposited sediment, turbidity was beneficial to newly settled *Orbicella faveolata* recruits, likely because it reduces the amount of light reaching the light-sensitive recruits. The recruits were exposed to 20 μmol photons $m^{-2}s^{-1}$ of light (which is already considerably low and typical of more shaded areas), but which was then further reduced due to fine grain sediment particles suspended in the water column. Therefore, in low turbidity treatments, corals were exposed to relatively higher light levels (closer to 20 μmol photons $m^{-2}s^{-1}$), while in high turbidity treatments corals were exposed to lower light levels. Recent studies suggest that coral recruits display higher survival when reared in lower light levels than those ideal for adults (Abrego et al. 2012, McMahon 2018). In shallow waters where light irradiance levels are high, coral larvae often prefer settling on the underside of tiles where light levels are lower (Birkeland et al. 1981, Rogers 1984, Babcock and Mundy 1996, Chamberlain et al. 2015), while in deeper and turbid areas larvae preferably settle facing upwards (Bak and Engel 1979; Harper 2017). Specifically, *Orbicella faveolata* larvae settle preferably on the underside of settling plates, which suggests that they prefer shaded areas with lower light (Szmant and Miller 2006). In this experiment, the larvae primarily settled on the groovy side of settlement tiles, as opposed to the smooth side of the tile. The rugosity from the grooves provide extra shading for the newly settled recruits and are more similar to crevices, where larvae typically settle in the field. It is likely that the larvae settle in crevices where light levels are low, then as the recruits grow and age, they eventually grow out of the crevice, at which point they are exposed to higher light levels.

The similar mortality trends obtained in both newly settled and six-week-old recruits in response to high turbidity suggest that the presence of symbionts did not diminish light sensitivity in coral recruits up to six weeks. Six-week-old recruits exhibited the highest survival in the high turbidity treatment, suggesting that the reduced light caused from suspended sediment is beneficial to both aposymbiotic and symbiotic recruits. This is contrary to our hypothesis that the older six-week-old recruits with symbionts would be able to be better able to withstand the higher light levels in the low turbidity treatments than the aposymbiotic recruits because they possess protective MAAs. It is possible that in the low turbidity treatments (when the symbiotic recruits were experiencing higher light levels), symbionts potentially became a burden when the symbionts were exposed to light and the corals were not feeding heterotrophically. Symbionts within coral tissues undergo photosynthesis, then release fixed carbon to the coral host to use for energy. Then in return, corals give symbionts nutrients from metabolic waste products, which aid in symbiont photosynthesis. However, when symbionts are exposed to light and photosynthesizing, if the corals are not feeding heterotrophically, the corals likely do not have enough nutrients to give the symbionts. In order to give nutrients to the symbionts to help them photosynthesize, the corals might have to use their energy reserves in order to give nutrients to the symbionts. It is likely that the six-week-old symbiotic recruits still were not feeding heterotrophically. While they were fed once per week, the recruits still did not have fully developed tentacles, thus preventing them to feed. Therefore, in the low turbidity/higher light treatments, the symbionts likely became a burden and depleted the coral’s energy reserves, leading to high mortality. While turbidity is typically a negative stressor for adult corals (Rogers 1990, Fabricius 2005, Erftemeijer et al. 2012), the lower light levels associated with high turbidity seem to be advantageous for newly settled and six-week-old coral recruits. However, recruits will require progressively higher light levels as they grow and develop (McMahon et al. 2018), so it is likely that there will be a shift throughout their lifecycle to where high turbidity changes from being beneficial to harmful to coral survival. This switch will likely occur when recruits are able to feed heterotrophically and do not have to use, and eventually deplete, their energy reserves in order to give symbionts the essential nutrients needed for photosynthesis.

While the lower light associated with higher turbidity is beneficial for coral recruits, the synergistic effects of high turbidity and the associated deposited sediment are harmful to newly settled *O. faveolata* recruits. Since turbidity is always coupled with deposited sediment (Pavanelli and Bigi 2005), this is more representative of the real conditions coral recruits would be exposed to during dredging or coastal construction activities. The higher mortality in the high turbidity and sedimentation treatments can be attributed to the sediment smothering corals, clogging coral recruit feeding structures, and/or creating an anoxic environment around the corals from bacterial growth (Rogers 1990; Fabricius 2005; Erftemeijer et al. 2012). In order to protect themselves from smothering, corals can remove sediment actively and/or passively (Lasker 1980). In areas with strong currents and wave action, water movement can help prevent or remove sediment that has settled on the corals. However, larger grain sizes are more likely to remain settled, while the fine grain sizes become resuspended in the water column. When passive sediment rejection via water movement is not sufficient, corals can actively remove sediment through mucus secretion and tentacle movement (Hubbard and Pocock 1972). Many of the newly settled recruits had not yet developed tentacles, thus, sediment rejection for newly settled coral recruits is likely not as effective. The high mortality of the coral recruits in the high turbidity and deposited sediment treatments is likely due to the recruit's inability to effectively remove sediment. While low levels of sediment and turbidity seem best for the survival of *O. faveolata* recruits, levels over 8.2 NTU coupled 50 mg cm^{-2} of deposited sediment were not compatible with recruit survivorship due to the smothering of coral recruits from high sediment loads.

The absence of sediment altogether was highly deleterious for the newly settled *O. faveolata* coral recruits, likely because sediment prevents the overgrowth of macroalgae. The majority of the recruits in the 0 NTU/0 mg cm^{-2} treatment died by the second week with 100% mortality by week three, suggesting that the absence of sediment is not ideal for recruits. While not quantified, tiles in this treatment were observed to have excessive macroalgae as opposed to other treatments containing sediment, which likely caused the high mortality (Fig. 12). It is therefore likely that low levels of sediment are necessary for recruits as a means of deterring excessive macroalgal growth. While macroalgae growth is harmful for all life stages of corals, many studies suggest that macroalgae is especially harmful for recruits because of their small size (Nugues and Szmant 2006; Box and Mumby 2007; Moeller et al. 2017; Johns et al. 2018; Robbins 2018). Excess macroalgae can impact corals by overgrowing recruits and juveniles and has also been shown to reduce coral growth rates (McCook 1999; McManus and Polsenberg 2004). The macroalgae that grew on the tiles in this experiment was a “turf algae” (Fig. 12), while the green algae seen on the tiles found within the tile porous surface was likely non-toxic. On healthy, pristine reefs, herbivorous fishes and invertebrates graze on macroalgae, facilitating coral dominance on reefs. However, in overfished and over euthrophied reefs, macroalgae growth is accelerated as there are not enough herbivores to control them (Burkepile and Hay 2010; Hoey and Bellwood 2011). The constant cycle of decreased coral recruitment and increased macroalgal growth can lead to a “phase shift” from a coral dominated reef to a macroalgae dominated reef. Sediment can likely benefit coral survival by preventing macroalgae growth, as increased sediment reduces algal growth and survival (Galarno 2017). Deposited sediment and the associated increase in turbidity may prevent macroalgae growth by reducing light available for photosynthesis, preventing a stable substrate for the algae to grow on, and smothering the algae (Umar et al 1998; McCook 1999). Since an environment with no sediment is not a realistic setting for coral recruits, a low amount of sediment seems to be beneficial for survival and algal growth prevention, especially for the early life stages of corals.

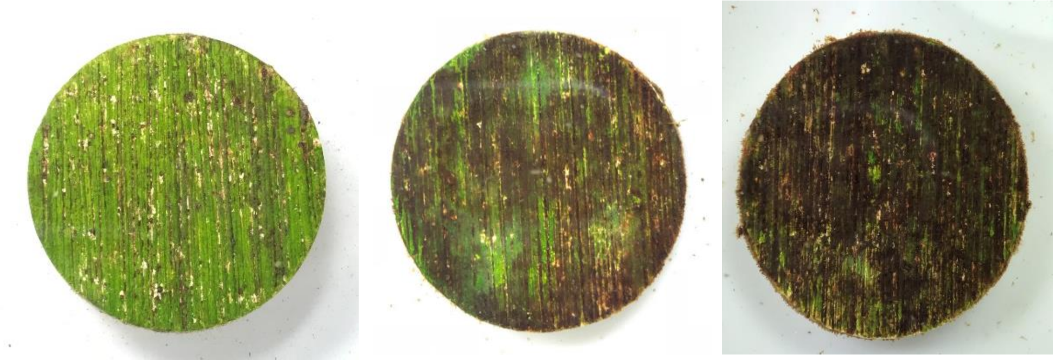


Figure 12. Tiles from the 29.1 NTU/ 220 mg cm^{-2} (left), 8.2 NTU/50 mg cm^{-2} (middle) and 0 NTU/ 0 mg cm^{-2} (right) treatments. (all upward facing) The tile from the 29.1 NTU/ 220 mg cm^{-2} treatment has less brown macroalgae growth than the 0 NTU/ 0 mg cm^{-2} treatment.

Growth rates of newly settled recruits were not significantly different between turbidity and deposited sediment treatments. The recruits were fed weekly; however, their tentacles were not fully developed so they likely were not able to feed heterotrophically. Also, the majority of newly settled recruits never acquired symbionts. Therefore, the recruits likely were allocating their energy reserves solely to survival and did not have enough energy to grow and develop. In addition to low energy reserves, the recruits were secreting their skeleton around the deposited sediment surrounding them (Fig. 13). This caused their skeleton to be heightened (observed, but not quantified), rather than spread out over more surface area, potentially to protect themselves from the sediment. Their heightened skeleton may cause latent effects in the future by further preventing growth or inhibiting feeding. Morphological changes in response to deposited sediment have also been observed in adult corals, such as a more "knobby" growth form to help prevent deposited sediment build-up rather than flat, plate-like forms (Barnes 1972; Foster 1980). It may be that the *O. faveolata* recruits are adopting a different growth form in response to their environment. Further research is needed to determine the latent effects of a heightened skeleton caused from coral recruits developing in a high turbid and deposited sediment environment.

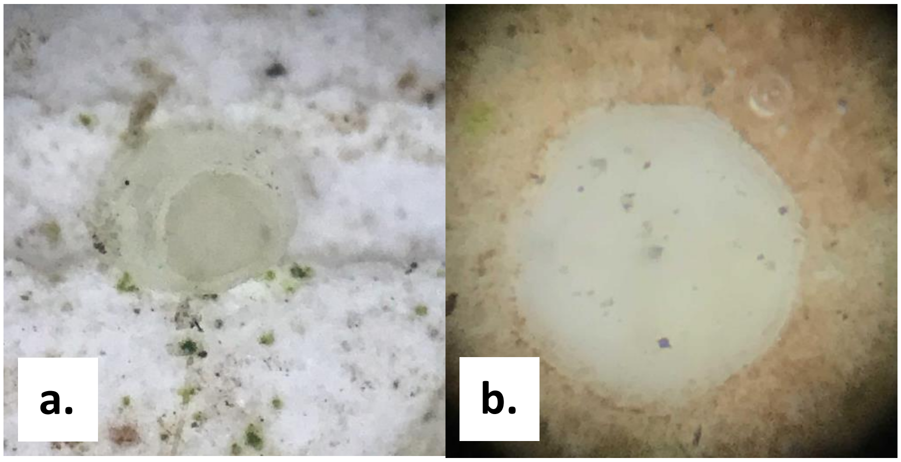


Figure 13. a) Two-week-old coral recruit with a heightened skeleton from depositing its skeleton around high sediment levels. b) Two-week-old coral recruit with a normal deposited skeleton from low sediment levels.

In order to prevent additional coral mortality and sustain depleted populations, it is essential to prevent unnecessary stress on the early life history stages of *O. faveolata* corals. One way to alleviate further stress is by reducing local stressors, such as increased sediment and turbidity. For this endangered and threatened species, recruits already experience low survival in natural conditions (Szmant and Miller 2006). Based on these results, and in order to prevent excessive deposited sediment on coral recruits, the Environmental Protection Agency should revisit the current allowable 29 NTU standards for the maximum allowable turbidity during dredging and coastal construction events. Although this study suggests that the low light associated with turbidity is beneficial for coral recruits, turbidity is a proxy for deposited sediment (Fig. 14). Therefore during coastal construction operations, high turbid waters are accompanied with high levels of deposited sediment which are harmful for all coral life stages. Since the highest survival was in the 27.7 mg cm^{-2} and 50 mg cm^{-2} deposited sediment treatments, the associated turbidity with these sediment values were 3.4 and 8.2 NTU, respectively. Therefore, to prevent large amounts of sediment deposited on coral reefs during coastal construction, turbidity should not exceed 8.2 NTU, as coral recruits cannot survive the associated deposited sediment levels higher than 50 mg cm^{-2}. Similar turbidity and deposited sediment thresholds have been observed for other species. Fourney and Figueiredo (2017) suggest that *Porites astreoides* recruit survival was significantly reduced above a turbidity level of 7 NTU and *Acropora cervicornis* recruit mortality increased at turbidity levels above 5.35 NTU (Robbins 2018). It is clearly evident that coral recruits cannot withstand the high deposited sediment levels associated with high turbidity, and the maximum allowable turbidity levels should be greatly reduced in order to prevent recruit mortality.

In addition to revising the maximum allowable turbidity levels during dredging and coastal construction, other factors should be taken into consideration during these operations. In this experiment, recruits were only exposed to turbidity and deposited sediment levels for five weeks. But in the field corals may be exposed to elevated levels for months, or even years (Jordan et al. 2010; Barnes et al. 2015). Therefore, we need to reduce the duration of coastal construction events in order to prevent the constant exposure of high sediment loads and stress on corals. Not only do turbidity and deposited sediment affect coral recruits as shown in this study, they also affect all coral life stages. Suspended sediments can interfere with gametes during fertilization (Gilmour 1999; Humphrey et al. 2008; Ricardo et al. 2016) and deposited sediment can cover available substrate or settlement cues used for coral settlement (Babcock and Davies 1991; Gilmour 1999; Babcock and Smith 2000; Storlazzi et al. 2015; Ricardo et al. 2017). Coastal construction should not be allowed during and the first few months after spawning events in order to prevent reduced settlement success from suspended particles and inhibited coral recruitment from high sedimentation levels. In addition, it is likely that this study may still be underestimating the negative effects of deposited sediment. The coral recruits in this study were exposed to a realistic sediment composition excavated during dredging, however, the sediment used was dried in order to remove any microscopic organisms and organic matter. Pollutants and volatiles from runoff can be buried within sediments, which are then reintroduced into the environment during coastal construction activities and cause eutrophication (Todd et al. 2010). Also, when high nutrient silt settles on top of coral polyps, this can cause microbial growth around the polyps and mortality of coral tissue (Weber at al. 2006). Managers should consider the possible impacts of nutrients within the sediment that are reintroduced to nearby environments during construction events. In addition to restricting deposited sediment, rules and regulations should be established to prevent overfishing of herbivorous fishes to inhibit macroalgae competition. By reducing these local stressors, managers can hopefully increase coral recruit survival and reef persistence in the future.

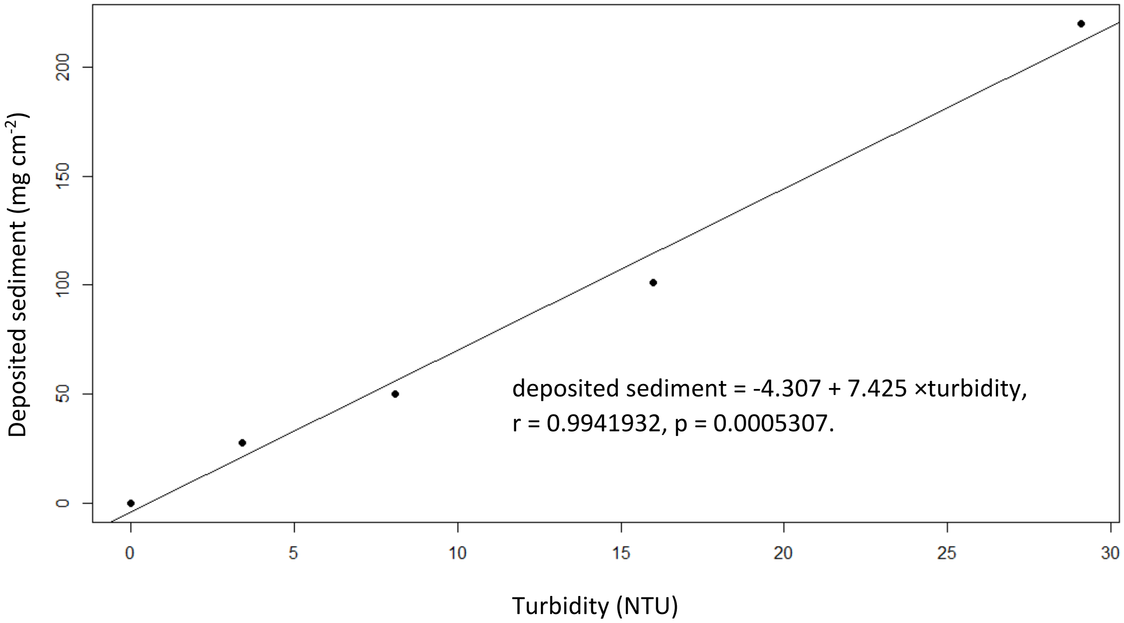


Figure 14. The relationship between turbidity levels and the associated deposited sediment levels for the following sediment grain size composition: 0.23% >2000 µm, 3.84% 500-2000 µm, 50.81% 180-500 µm, 37.01% 63-180 µm, 8.19% <63 µm.

Acknowledgements

I would like to thank my major advisor, Dr. Joana Figueiredo, and committee members, Dr. Brian Walker and Dr. Rachel Silverstein, their guidance and advice. I would also like to thank Dana Williams for the *Orbicella faveolata* larvae for this experiment and the past and present members of the Marine Larval Ecology Laboratory for their help and support. Lastly, I would like to thank my wonderful friends and family for their constant encouragement.

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